The growth benefits of aggressive behavior vary with individual metabolism and resource predictability

Hoogenboom, Mia O.; Armstrong, John D.; Groothuis, Ton G. G.; Metcalfe, Neil B.

Published in:
Behavioral Ecology

DOI:
10.1093/beheco/ars161

Behavioral Ecology
doi:10.1093/beheco/ars161
Advance Access publication 28 September 2012

Original Article

The growth benefits of aggressive behavior vary with individual metabolism and resource predictability

Mia O. Hoogenboom,[a] John D. Armstrong,[b] Ton G. G. Groothuis,[c] and Neil B. Metcalfe[a]
[a]Institute of Biodiversity, Animal Health & Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow G12 8QQ, Scotland, UK, [b]Marine Scotland Science, Freshwater Laboratory, Pitlochry, PH16 5LB, Scotland, UK, and [c]Behavioural Biology, Institute of Behavioural Neuroscience, University of Groningen, Nijenborgh 7, 9747 AG, Groningen, Netherlands

Differences in behavioral responses to environmental conditions and biological interactions are a key determinant of individual performance. This study investigated how the availability and predictability of food resources modulates the growth of animals that adopt different behavioral strategies. Results show that, irrespective of the feeding regime, the growth of juvenile brown trout increased with the expression of active foraging behavior and, similarly, with increasing use of shelter. Conversely, territorial aggressive behavior only promoted growth when food resources were spatially and temporally predictable, and only for individuals that had high metabolic rates (when compared with their low metabolic rate siblings). Thus, this study shows that only certain behaviors are associated with variation in the physiology of individuals. Moreover, only certain behaviors associate differently with growth under different environmental conditions. These results are partially consistent with the hypothesis that environmental variability promotes the coexistence of alternative behavioral phenotypes. However, some behaviors enhanced growth irrespective of feeding regime, and we did not identify a set of conditions where fish with low resting metabolic rate (RMR) outperformed their high RMR siblings. Hence, additional layers of environmental variation are likely to be required for individuals with low RMR to show maximal growth performance. *Key words:* aggression, animal personality, behavioral strategy, dominance behavior, food predictability, resting metabolic rate, *Salmo trutta*. *[Behav Ecol]*

INTRODUCTION

The phenotypes of individuals can vary substantially within populations. Over the past decade, ecological research has fostered awareness that even when individuals have very similar morphology, they can vary in their behavioral responses to the environmental conditions and biological interactions they experience (e.g. Sih et al. 2004). Such variations in individual behavior can have a substantial influence on fitness (Dingemanse and Réale 2005; Bell 2007). For instance, animals that have a high rank within a dominance hierarchy can benefit from faster growth rates (Nakano 1995; Buchner et al. 2004) and increased reproductive output (von Hulst et al. 2002; Ang and Manica 2010). Despite increasing research on animal "personalities," whether and how the fitness consequences of behavioral variation depend on environmental conditions is poorly understood (Smith and Blumstein 2008; but see Both et al. 2005). To address this knowledge gap, in this study, we investigated whether behavior has different effects on growth depending on environmental conditions (food availability and predictability) and on the physiology of individuals (resting metabolic rate [RMR]).

Among-individual variation in behavior has been widely studied in the context of foraging activity. Early work on freshwater fish feeding on invertebrate drift in streams revealed a bimodal distribution of foraging activity, with individuals tending to adopt one of two different foraging strategies (sedentary vs. mobile) within a narrow range of environmental conditions (McLaughlin et al. 1992; Nakano 1995). Further investigations of the same study system revealed that highly active fish tended to feed at pool surfaces, and that both highly active and highly sedentary fish were more aggressive than those with intermediate activity levels (McLaughlin et al. 1999). Moreover, individuals that were more active in the field were also quicker to explore novel environments during laboratory tests (Wilson and McLaughlin 2007). Similar patterns have been observed in other organisms, with foraging range also associated with explorative behaviors in birds (van Overveld and Matthysen 2010).

Among-individual variation in physiological status, such as differences in hormone levels or metabolic rates, is often associated with variation in animal behavior (e.g. Careau et al. 2008; Biro and Stamps 2010). For instance, aggression is associated with levels of androgen hormones (Nelson 2000), and risk-taking behavior is related to stress hormone concentrations (Martins et al. 2007). Moreover, a strong relationship between dominance behavior and metabolic rate is observed in many species (e.g. Brown et al. 2003). In birds, RMRs (i.e. the basal metabolic costs of maintaining life) tend to be higher in dominant individuals (*Cinclus cinclus*; Bryant and Newton 1994) although subordinate individuals can also have higher metabolic

Address correspondence to M.O. Hoogenboom, who is now at School of Marine and Tropical Biology, James Cook University, Douglas, QLD 4811, Australia. E-mail: mia.hoogenboom1@jcu.edu.au
Received 5 June 2012; revised 19 July 2012; accepted 23 August 2012.

rates than dominants due to costs of remaining vigilant to the presence of dominants (Senar et al. 2000). In fish with approximately equivalent body size, dominance behavior is generally positively associated with metabolic rate, with this phenomenon now widely documented for several salmonid species (Burton et al. 2011a).

Food availability is likely to interact with individual metabolic rate to determine the fitness consequences of behavior because sustaining a high metabolic rate together with high levels of activity requires adequate food resources (Burton et al. 2011a). Previous research has shown that dominant and active individuals have a higher cost-of-living because their metabolic costs are higher (Metcalfe 1986) and because they spend a greater proportion of their time foraging and defending their territory (Höjesjö et al. 2004; Finstad et al. 2007). These observations give rise to the prediction that highly active and dominant individuals will have enhanced fitness only when food is abundant throughout their habitat or, where food availability is patchy throughout the environment, the location of "good" patches is spatially and temporally predictable (Armstrong et al. 2011; Reid et al. 2012). Under such conditions, increased energy intake gained through monopolizing food resources can compensate for higher maintenance and activity costs (Álvarez and Nicieza 2005). The converse prediction is that the energy costs of activity and aggression will constrain dominance behavior when food levels are critically reduced and lead to a situation where subordinate/inactive individuals, with lower metabolic rates, can outperform dominants (Clarke 1992). Subordinates potentially obtain a similar growth and/or survival advantage when food availability is temporally or spatially unpredictable (Bang et al. 2007). Nevertheless, predicting the relative performance of individuals with different behavioral phenotypes is complicated by the fact that subordinates may perform increasingly well as food becomes more abundant and dominants become satiated (Armstrong et al. 2011).

This study quantifies the consequences of among-individual variation in behavior for the growth of juvenile brown trout (*Salmo trutta* L.). Specifically, we aimed to test the effects of metabolic rate, individual size, and feeding regime on both trout behavior and growth. To meet this objective, we quantified the relationship between metabolic rate and individual behavior, assessed whether juvenile trout behavior differed in response to the different feeding regimes, and evaluated which physiological and behavioral strategies conferred highest growth under different experimental conditions. Herein, we measured individual growth as a proxy for fitness because increased growth enhances survival of juvenile trout during their first summer after hatching (Elliott 1990; Armstrong and Nislow 2006). Overall, this paper addresses the hypothesis that the coexistence of different behavioral strategies within populations is maintained via the relative benefits of high versus low metabolic rates under conditions with different food availability and predictability (e.g. Wilson 1998; Burton et al. 2011a).

MATERIALS AND METHODS

Overview

We used an experimental approach to test how the behavior of juvenile brown trout varied in response to food availability and predictability, whether behavior differed between individuals with high versus low metabolic rate, and how food regime, behavior, and metabolic rate interact to determine juvenile growth rates. Juvenile trout ("fry") were sourced from Almondbank Hatchery (Perthshire, Scotland) and were first generation laboratory-reared offspring of wild fish caught from areas close to spawning-streams feeding into Loch Broom (Scotland). At the time of the experiment, in August through September 2009, juveniles weighed approximately 2 g (range 0.6–3.3 g, length range 38–65 mm). Prior to the experiment, fry were transferred to aquarium facilities at the University of Glasgow where they were held at densities of 0.5 g l^{-1} in large fiberglass tanks (250 l) equipped with pumps to generate water flow and with large sections of opaque plastic tubing to provide shelter. Water temperature was maintained at 12 °C (range 11.4–13.4 °C) using room air conditioners. Fry were fed daily with frozen bloodworm *ad libitum* prior to the experiment.

A minimum of 7 days before screening for RMR, fry were anaesthetized and individually marked using Visible Implant Elastomer (Northwest Marine Technology, Shaw Island, Washington, USA), with one or two color tags (in one of 24 unique combinations) placed between the dorsal fin and the lateral line. A total of 50–60 individuals from each of 7 different full-sibling groups (families) were used for behavioral observations, of which 48 per family were used for measurements of metabolic rate. RMR was measured in 16 fish from a single family per day. To investigate whether individuals with high metabolic rates have reduced growth rates when food availability is restricted and unpredictable we selected, from each group of 16 fish, the 4 fish with the lowest and the 4 with the highest RMR for their size. These 8 sibling fish were then placed, as a group, in an experimental tank under one of three feeding regimes (see Experimental setting) and monitored for behavior and growth over a 2-week period. The procedure was replicated 3 times for each of the 7 families (with a different feeding regime each time), so that there was one group of fish from each family for each feeding regime. Replicate groups were established at a rate of 4 per week for 4 weeks followed by 5 replicates in the final week and were stratified by families and feeding treatments.

Metabolic rate measurements

Metabolic rate was measured using flow-through oxygen respirometry, following the procedure outlined in Cutts et al. (2001). In summary, individual fry were placed in 16 plastic chambers (10 ml volume) with constant water flow at 0.3 l h^{-1} (± standard deviation [SD] 0.02) and in a darkened environment. Flow rate was controlled by a peristaltic pump (Masterflex L/S 100 rpm digital drive with 3 × 8 channel pump heads, Cole Parmer, Hanwell, UK), and the water supply came from a header tank containing oxygenated water. Fish were allowed to settle in the chambers overnight, with measurements commencing 17–20 h later. Previous studies of juvenile salmonids have demonstrated a stable oxygen consumption rate after this period of acclimation (Cutts et al. 2001). The reduction in oxygen concentration due to fry respiration was measured with a Fibox 3 temperature-compensated oxygen meter (Loligo Systems, Tjele, Denmark). To do this, a calibrated flow-through cell with integrated oxygen sensor (PreSens, Regensburg, Germany) was connected to the outflow from each chamber, and oxygen content was monitored during a 5–8-min period. Oxygen consumption rates ($\dot{V}O_2$, ml O_2 h^{-1}) of individual fish were calculated as:

$$\dot{V}O_2 = V_W \cdot \Delta C_W \cdot \beta O_2, \quad (1)$$

where V_W is flow rate (l h^{-1}), ΔC_W is the difference in oxygen concentration between water inflow and outflow, and βO_2 is the capacitance of oxygen in the water (ml O_2 l^{-1}). Inflow oxygen concentration was determined from measurements of control chambers containing water but no fish that

were taken prior to, half-way through, and immediately after measurements of each batch of 16 fish. Oxygen consumption rates of each fish were measured twice, with a minimum interval of 1 h between measurements, and a third reading was taken if the second value was not within ±20% of the first. When this occurred (for 29% of the 336), all 3 values were averaged to obtain the metabolic rate measure for each fish. Water temperature during respirometry averaged 14.5 °C (± SD 0.5), and small changes in oxygen capacitance due to temperature variation were accounted for in the metabolic rate calculations. Immediately after respirometry, fry were anaesthetized, weighed (±0.001 g), and measured for standard length (snout to beginning of caudal fin, L_S, ±0.1 mm). At the end of the 2-week period, all fry were anaesthetized, weighed (±0.001 g), and measured (L_S ± 0.1 mm) for determination of growth rate. We note that although growth rate is presented as change in absolute size, none of the outcomes differed if proportional growth was used instead (analyses not shown).

Determination of high versus low RMR individuals

Due to allometric scaling between metabolic rate and body size, high and low RMR individuals were defined from residuals of the relationship between ln(RMR) and ln(mass). To do this, ln(RMR) was regressed on ln(mass) for each batch of 16 fish and regression residuals (observed – predicted) were calculated for each individual fish. Within each batch, the 4 fish with the most negative residuals were selected to form the low RMR group (i.e. individuals with lower metabolic rate than expected based on size) and those with the 4 largest positive residuals were selected as the high RMR group. Analysis of mass-specific RMR (i.e. independent of the residual analysis) was performed at the completion of the experiment and confirmed that metabolic rate (log-transformed) strongly differed between RMR groups (mixed-effects analysis of variance [ANOVA], $F_{(1,146)} = 295$, $P < 0.001$, with measuring batch and family as random factors).

Experimental setting

Following screening of metabolic rate, the 8 fish selected from each batch were placed as a group into a section of an aquarium system (total volume 200 l) consisting of 2 replicate racks of 3 glass tanks (180 × 25 × 20 cm) that were stacked above one another on aluminum racks and linked together by tubing. A pump at the base of the system recirculated water and established a consistent, unidirectional flow (1.28 ± standard error [SE] 0.03 cm s^{-1}) through the entire system. All tanks were supplied with the same recirculating water (fitted with a UV sterilizer and a sump tank and filter to maintain water quality) so that any chemical cues were equally, and continuously, mixed throughout each set of tanks. Each tank was fitted with a white plastic longitudinal divider producing a total of 12 compartments with dimensions 180 (length) ×12.5 (width) ×15 cm (depth). Compartment dimensions (0.23 m^2) approximated the feeding territory size of 4 fish, based on Grant and Kramer (1990) and an initial mean body length of 4 cm (predicted territory size of 0.05 m^2). Each compartment was equipped with 3 feeders, equally spaced throughout the central three-fifth of the compartment, and a translucent-plastic shelter was placed in the downstream and upstream one-fifth of the compartment (Figure 1). If high-ranking fish formed feeding territories around these 3 feeders, then each of the 3 territories would have an area of 0.14 m^2, 2.5x greater than the predicted territory size of an individual fish. Compartments were designed to promote interactions between individuals but to prevent a single individual from monopolizing all of the food outlets. Approximately, 15% of the water was changed daily during routine cleaning.

Three feeding regimes were designed to test how food availability and predictability affected fish behavior and growth. Food availability treatments (high and low) corresponded to 100% of the maximum daily food intake and 10% above the maintenance food requirement, respectively. Each group of fish was fed commercial food pellets (EWOS, 5.1 cal mg^{-1}) delivered into experimental compartments using belt-feeders. These were refreshed with food and placed into position at the same time each day (9:30 AM). All belt-feeders delivered food over a 12-h period to each of the feeders in each compartment, but the amount of food and timing of delivery differed between treatments. The high ration predictable (HP) feeding regime provided 32 mg $fish^{-1}$ d^{-1} (based on Elliott 1975a), divided into 4 equal portions per day, spread across 3 feeders per tank, with food delivery taking approximately 10 min and occurring at the same time each day. The low ration/predictable (LP) feeding regime delivered food portions in the same way as above except that the daily ration was reduced to 13 mg $fish^{-1}$ d^{-1} (based on Elliott 1975b). Finally, a low ration/unpredictable (LU) feeding regime also provided 13 mg $fish^{-1}$ d^{-1}, but the timing and location of food delivery was varied. To do this, the ration supplied to each tank was apportioned differently between the 3 feeding locations each day and positioned haphazardly such that the timing of food delivery, and also portion size, also differed between days.

Behavioral observations

Groups of fish (n = 21 in total) were allowed to acclimatize for the first 5–6 days of the 2-week experimental period after which a suite of behavioral traits were observed during a combination of scans (point measurements of all individuals) and focal observations (continuous monitoring of individual fish). All observations were made by a single observer standing stationary 1 m away from each experimental tank. The observer remained stationary in position for a minimum of 5 min prior to initiating each observation period. During this time, all fish were carefully observed to identify their color tags. The observer worked blind with respect to the RMR category of individual fish. Throughout the experiment, 4 fish died of unknown causes partway through the observation period. These individuals were excluded from the analyses.

Scans were conducted on each of 4 days throughout the experimental period, with the activity and location of all individuals within each tank recorded at 4 times throughout the day (minimum of 1 h between observations). Activity was recorded as one of three mutually exclusive behaviors: changing location (moving more than one body length during a 3 s time period), stationary swimming in the water column, or resting immobile. Location was recorded as one of 34 different positions within the tank, as follows: 4 vertical levels by 8 horizontal sections plus 2 within-shelter positions (Figure 1). Shelter occupancy by individual fish was also recorded during these scans. Focal observations monitored and recorded individual behavior (activity, location, and shelter use as outlined above) every 20 s for 10 min. These observations were made for 4 individual fish per tank per day, with the first set of 4 fish selected haphazardly on the first day of observation and the remaining individuals observed on subsequent days. Focal observations for each fish were collected twice during the experiment.

Data from scans and focal observations were used to quantify 5 different aspects of behavior. Territory size was assessed from the total number of zones within which a fish was observed over the whole observation period, and territory quality was

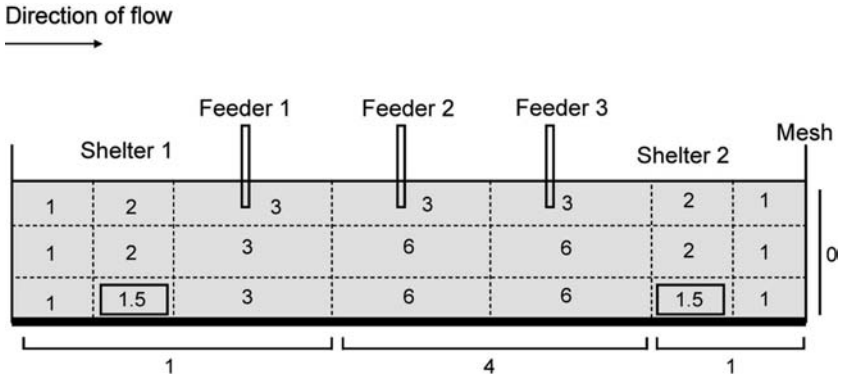

Figure 1
Schematic diagram (side view) of the experimental tanks. Numbers indicate scoring system for the stream position component of behavior (see text) and numbers at the base of the diagram indicate the position scores in cases where fish were stationary on the bottom of the tank.

calculated based on the locations of fish relative to the feeders within each tank. For territory quality, tank locations were scored as follows: locations in the water column downstream and below feeders 2 and 3 were given 6 points, and scores decreased with distance from feeding stations (see Figure 1). This system was based on Burton et al. (2011b) and Metcalfe et al. (2003) showing that the highest rates of food-capture by juvenile brown trout fry were achieved by individuals in the lower two-thirds of the water column immediately downstream from feeding sites. Activity was calculated from movement observations for each individual throughout the experimental period, with movement scored as 2 points for changing location, 1 point for stationary swimming, and 0 point for resting immobile.

Aggressive interactions between fish were recorded during a single 10-min period in the afternoon of day 9–11 of the experiment for each group. In addition, all aggressive interactions witnessed during scans and focal observations were recorded when both individuals involved in the interaction could be clearly identified. Only overt aggressive displays (chase and nip) were noted (e.g. Cutts et al. 2001). An aggression score was tallied from all observations of aggressive interactions. Scores were allocated based on Burton et al. (2011b) as follows: 2 points if a fish attacked and forced a submissive response, 1 point if a fish attacked but did not force a response, 0 point for an attacked fish that did not submit, and −1 point for fish submitting to an attack. Finally, shelter occupancy was scored over the experimental period by awarding 1 point for each occurrence of shelter use.

Data analysis

Principal components analysis (PCA) was used to identify the major axes of behavioral variation based on the multivariate correlation matrix and with all variables scaled and centered. PCA was used because we were primarily interested in reducing the behavioral variables into a smaller number of maximally informative components. Only variables with loading values greater than 0.4 on PCs were interpreted as contributing meaningfully to each PC, in accordance with common practice (Norman and Steiner 2008). The effects on growth rate of feeding treatment, metabolic rate, behavioral variation, and body size were assessed using linear mixed-effects analysis of covariance. In these analyses, family identity was included as a random effect, with feeding regime and metabolic rate group specified as fixed, categorical factors. Relative body mass (at the start of the observation period for each group) was included as a covariate and was converted to a z-score prior to inclusion such that relative mass represents the size of individual fish relative to others within their group, normalized by mean group mass. Variation in behavior was incorporated into these analyses by including PCA scores of individual fish as covariates. Concordance of the data with normality and homogeneity of variance assumptions of the analysis were assessed by visual inspection of normal QQ plots and plots of fitted values versus residuals. All analyses were performed in R (R Development Core Team, 2010) using "prcomp" and "cor.test" for the PCA, and using "lme" within the package "nlme" for analysis of variance.

RESULTS

Among all of the fish used for the behavioral observations, linear regression of $\log_e$(RMR, ml O_2 g^{-1} h^{-1}) on $\log_e$(mass, g) explained 65% of the variation in metabolic rate, with the intercept (−1.84 ± SE 0.03) and slope (0.89 ± SE 0.06) both significantly different from zero ($P < 0.001$ in both cases). Mean mass-specific metabolic rate ranged from 0.20 to 0.26 ml O_2 g^{-1} h^{-1} (i.e., 1.3-fold) between families, with this variation being smaller in magnitude than the 2–3-fold (average range 0.14 to 0.35 ml O_2 g^{-1} h^{-1}) variation within families.

The behaviors observed here for juvenile trout were relatively strongly inter-correlated (Table 1), with activity strongly positively correlated with territory quality ($r = 0.6$) and negatively correlated with shelter use ($r = -0.56$, Table 1). Behavior was generally consistent among the different feeding treatments, both with respect to the average scores, and the range of scores observed for each behavioral trait (Figure 2). PCA identified 3 components (PCs) that explained 85% of the variation in behavior (48% on PC1, 22% on PC2, and 15% on PC3). We did not observe any strong clustering of individuals that would indicate the presence of discrete behavioral strategies. Instead behavior varied along a continuum for all 3 PCs.

Table 1
Correlations between behavioral variables

	A	T	X	Q	S
Activity (A)		0.37	0.48	0.60	−0.56
Territory size (T)	<0.001		−0.03	0.28	−0.30
Aggression (X)	<0.001	0.71		0.40	−0.17
Territory quality (Q)	<0.001	<0.001	<0.001		−0.19
Shelter use (S)	<0.001	<0.001	<0.05	<0.05	

Values above the diagonal are correlation coefficients (Pearson's *r*) and values below the diagonal represent statistical significance level (degrees of freedom [df] = 162 in all comparisons).

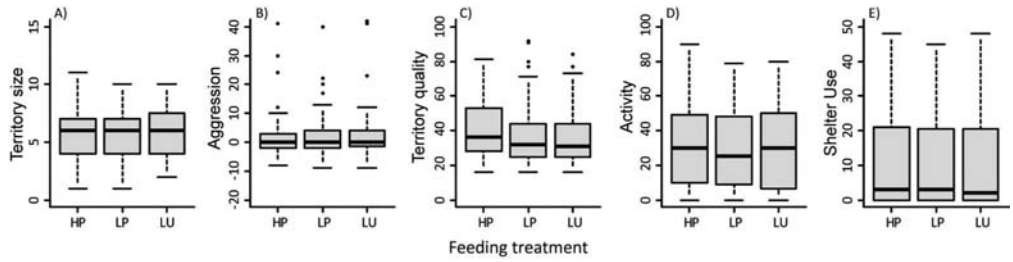

Figure 2
Variation in behavior of juvenile brown trout according to feeding treatment showing the distribution of scores for territory size (A), aggression (B), territory quality (C), activity (D), and shelter use (E). Boxplots show median (solid bar), inter-quartile range (box), and whiskers have length 1.5 times the inter-quartile range and points represent outlying values. Feeding treatments are LP: low ration, predictable; LU: low ration, unpredictable; and HP: high ration, predictable.

PC1 was strongly negatively associated with variation in activity and territory quality (Table 2), although shelter use also contributed to this component. Overall, this PC separated individuals along a scale of decreasing foraging activity: fish that obtained a strongly negative score on this axis spent a large proportion of their time actively swimming in close proximity to the feeding stations. PC2 was very strongly associated with territory size and aggression, with the direction of these effects positive for aggression and negative for territory size (Table 2). Overall, PC2 separated individual trout along an axis of increasing territoriality: fish with high scores on this axis aggressively defended a small patch of space within experimental tanks. PC3 was most strongly associated with variation in shelter use (Table 2), with fish that had high scores on this axis tending to spend a greater proportion of time within shelters.

Growth rate, measured as change in mass over the duration of the experimental period, ranged from −29 to 78 mg d^{-1} (mean 8 ± SD 20). This broad range, and the fact that negative growth was observed in several individuals, suggests that there was strong competition for food within the experimental groups. Growth rate was, on average, influenced by food quantity rather than predictability (Table 3, growth of trout under the maintenance diet was significantly lower than under the maximum diet regardless of the predictability of the food supply). The effect of the feeding regime did not differ between individuals with high and low metabolic rate for their size (RMR group by feeding regime interaction term, $F_{1,144} = 0.18$, $P = 0.84$) but, overall, individuals with low RMR grew slower than their high metabolic rate siblings ($F_{1,146} = 8.4$, $P < 0.01$). A fish's size also significantly influenced its growth rate with larger individuals tending to have higher growth ($F_{1,146} = 9.6$, $P < 0.01$, Table 3).

Table 2

PCA of juvenile trout behavior showing correlations between the identified components (PC1–3) and each of the measured behavioral traits, degrees of freedom (df) for statistical tests is 162 in all cases. Component loadings are also shown (i.e. correlations [Cor] standardized by component SD). Component SDs were equal to 1.6, 1.1, and 0.88 PC1, PC2, and PC3, respectively

Component	Variable	Loading	Cor.	*t*	*P*
1: Active foraging	Activity	−0.59	−0.91	−28	<0.001
	Territory quality	−0.48	−0.74	−14	<0.001
	Shelter use	0.41	0.64	10.7	<0.001
2: Territoriality	Territory size	−0.64	−0.67	−11	<0.001
	Aggression	0.64	0.67	11	<0.001
3: Shelter use	Territory size	0.46	0.40	5.6	<0.001
	Territory quality	0.52	0.45	6.5	<0.001
	Shelter use	0.71	0.62	10	<0.001

Table 3

Minimal mixed-effect model of effects of feeding regime (Treatment), RMR, relative body mass, and behavior on juvenile trout growth

Factor	dF	F	*P*
Intercept	1,146	37	<0.001
Relative mass	1,146	9.6	<0.01
RMR	1,146	8.4	<0.01
Treatment	2,146	34	<0.001
PC1 score	1,146	143	<0.001
PC2 score	1,146	15	<0.001
PC3 score	1,146	8.3	<0.01
Treatment × PC2 score	2,146	5.5	<0.01
Relative mass × RMR × PC2 score	2,146	3.6	<0.05

Family identity was included in the model as a random effect. Relative mass reflects standardized (within-group) *z*-scores and behavior is represented by PCA scores. Model simplification was implemented by backward deletion of nonsignificant terms in order of high–low-order interactions and *P* value. Model degrees of freedom (dF) are shown together with F statistics and probability values.

The ranking of individuals along the active foraging scale (i.e. their PC1 score) was strongly associated with growth rates (Figure 3). Similarly, shelter-association (PC3 score) had a positive influence on growth when all other effects were accounted for (Table 3, data not shown). The effect on growth of both of these behavioral traits was independent of individual size and consistent among all feeding regimes and RMR categories (interaction terms involving PC1 and PC3 were not retained in the minimal model, Table 3). However, within each experimental grouping, the individual that was identified as the most active forager (most negative PC1 score) had significantly higher growth than both territorial and shelter-associated individuals in its group (one-way ANOVA, $F_{2,24} = 14$, $P < 0.001$).

The effect of territoriality on growth depended on feeding regime (significant interaction between treatment and PC2 score, Table 3). Growth was positively associated with territoriality when food delivery was predictable, irrespective of whether a high food or maintenance diet was available (Figure 4A,4B), but was not related to territoriality in the unpredictable food treatment (Figure 4C). The slopes of the relationships between growth and PC2 were not significantly different for the 2 predictable food treatments (slope = 6.28 for HP and 6.34 for LP, SE of difference [HP vs. LP] = 2.4, $t = -0.02$, $P = 0.9$), but the relationship was significantly different under the low ration and unpredictable feeding regime (slope = −0.21 of LU, SE of difference [LU vs. LP] = 2.3, $t = -2.8$, $P < 0.01$). The effect of territorial behavior on growth also varied differently in response to body mass for individuals with high versus low metabolic rate (significant interaction

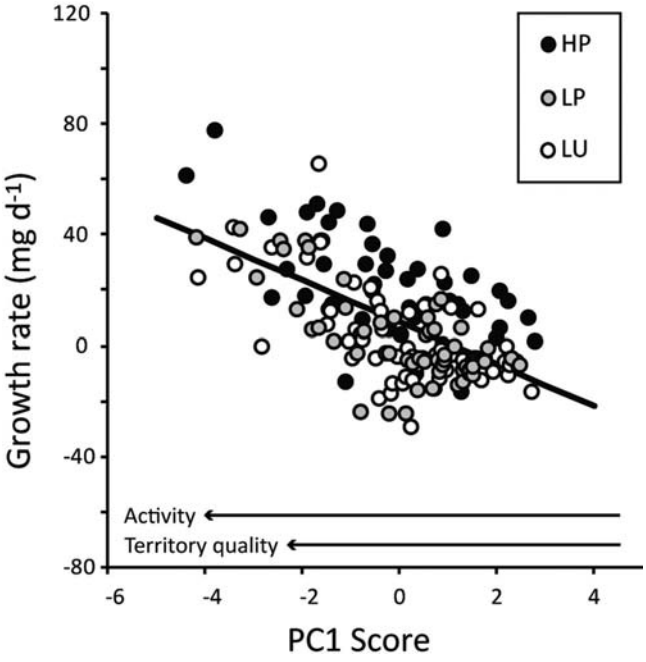

Figure 3
Relationship between expression of active foraging behavior (PC1 score) and growth rate for juvenile brown trout. PC1 scores are from PCA and points represent values for individual fish, with symbols denoting the different feeding treatments. Line is based on parameter estimates from the mixed-effects ANOVA (see Table 3).

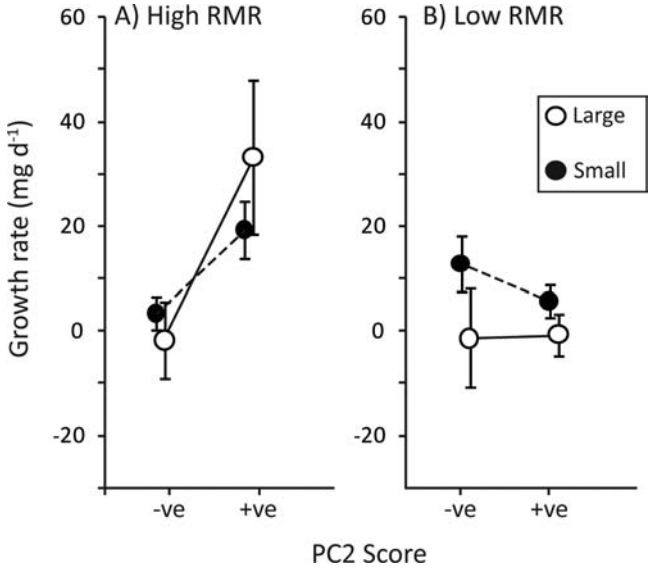

Figure 5
Interaction between relative body mass and metabolic rate determines the fitness benefits of territoriality. Points are means of 6 data points at the extremes of juvenile trout mass (large vs. small) and aggression behavior (PC2 score) within RMR groups (high vs. low). Continuous data are here plotted as categorical variables (for relative mass and PC2 scores) to aid visual interpretation.

between relative mass, RMR, and PC2 score, Table 3). For fish with high RMR, territoriality enhanced growth, and this effect was more pronounced for large compared with small individuals (Figure 5A). In contrast, territoriality did not enhance growth for fish that had low RMR, and small individuals had slightly higher growth than large individuals in this category (Figure 5B).

To determine how fish displaying particular combinations of behaviors ranked within the group pecking order, we identified the individual that was most clearly an "active forager" (with the lowest PC1 score), the individual that was the most territorial (with the highest PC2 score), and the individual with the highest shelter use (PC3 score) within each group (n = 21 groups), and then analyzed the outcome of pairwise aggressive encounters between these fish. Encounters between these 3 categories of fish accounted for 30% of the 379 aggressive interactions observed and occurred in 14 of the 21 groups. Among these encounters, 36% involved active foragers winning contests with shelter-associated individuals and 37% involved territorial individuals winning contests with shelter-associated individuals. Conversely, only 4% of the observed contests were won by shelter-associated individuals over either active foraging or territorial individuals. Within each experimental grouping, high RMR individuals were identified as the most active forager (most negative PC1 score) in 17 of the 21 trials (81%), whereas high RMR fish were identified as each of the most territorial fish or shelter-associated individuals in 12 of the 21 trials (57% for both categories). In summary, both active foraging and shelter-association enhanced growth irrespective of food availability, and active foraging behavior was most apparent in large fish with high RMR. Whether or not territoriality enhanced growth depended on feeding regime and on the body mass and metabolic rate of juvenile trout (Figure 6).

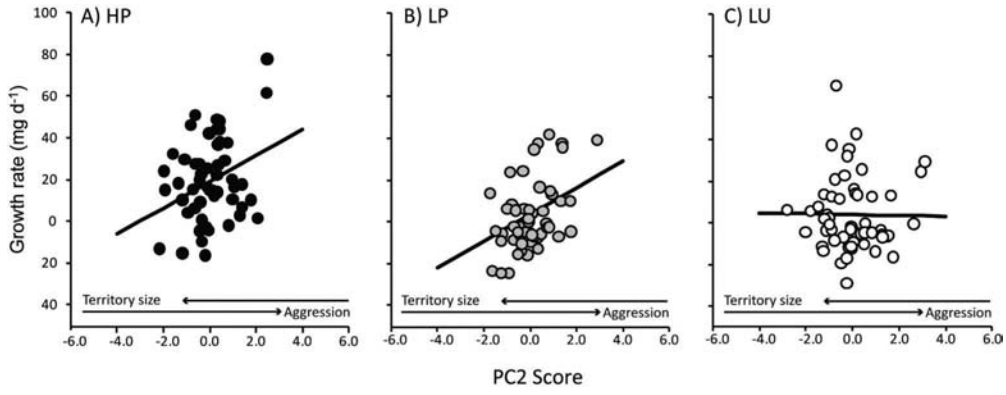

Figure 4
Relationship between expression of territorial behavior (PC2 score) and growth rate within different feeding regimes (A) high ration, predictable food supply, (B) low ration, predictable food supply, and (C) low ration, unpredictable food supply. PC2 scores are from PCA and points represent scores of individual fish. Lines are based on parameter estimates from the mixed-effects ANOVA.

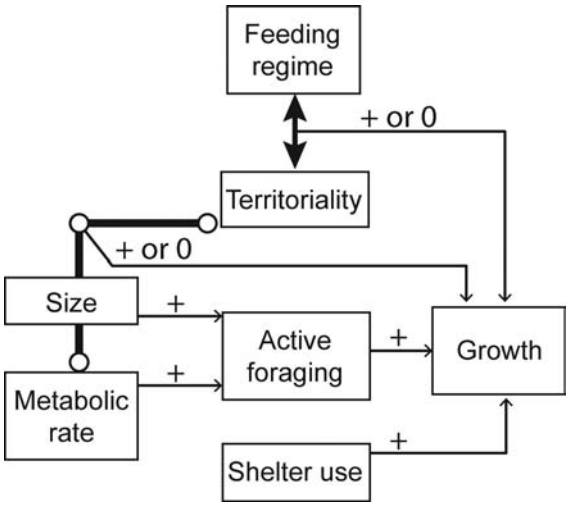

Figure 6
Summary of the observed effects of metabolic rate, feeding regime, and body size on juvenile brown trout behavior and growth. Plain arrows denote main effects, double-ended thick arrow denotes 2-way interactions between connected boxes, and circle ended arrows joining and passing through boxes denote 3-way interactions. Directions of these effects are signified by symbols denoting positive (+) or neutral (0) effects. Statistical analyses describing these relationships are presented in Table 3.

DISCUSSION

This study demonstrates that the benefits of territorial aggressive behavior depend on the predictability of food resources and also on the physiology of individual trout. Results showed that aggressive defense of small territories only enhanced growth when resources were predictable, and that, irrespective of food regime, the benefits of aggression were only evident for fish that had a high metabolic rate (and particularly for large individuals). In contrast, active foraging and shelter-association enhanced growth irrespective of food regime. Previous studies on freshwater fishes have quantified the behavioral variation within field and laboratory populations (McLaughlin et al. 1999; Martin-Smith & Armstrong 2002; Maclean et al. 2005; Steingrimsson and Grant 2011), but have not directly quantified how resource predictability mediates the relationship between behavior and performance. In a recent effort to address this knowledge gap, Reid et al (2012) showed that the relationship between metabolic rate and growth depends on the structural complexity of the environment, with physically complex habitats preventing dominant fish from displacing subordinates from good quality sites. This study is congruent with previous work showing that individual metabolism and behavior influence juvenile fish growth (e.g. Metcalfe et al. 1995; Reid et al. 2012), but we additionally show that only certain behaviors are linked to variation in metabolic rate (i.e. active foraging) and only certain behaviors influence growth performance differently under different resource regimes (i.e. territorial aggression).

Contrary to previous work showing that freshwater fish can display a bimodal distribution of foraging activity (McLaughlin et al. 1992), the juvenile trout in this study displayed a continuum of variation along 3 different behavioral axes (active foraging, territoriality, and shelter-association). When all 3 behaviors were included in the analysis of variation in growth rates, growth was significantly positively associated with each. Even though shelter-associated individuals were behaviorally subordinate to both active foragers and territorial individuals, and had lower average growth rates (3.9 mg d^{-1} ± 4.1 SE vs. 34±3.9 SE for shelter-associated and active foragers, respectively), the amount of time spent within a shelter was positively related to growth rate after controlling for the effects of active foraging and territoriality. A likely explanation for this result is that shelter-association requires lower energy expenditure on movement than active foraging or territoriality, and this potentially counteracts the reduced food acquisition associated with holding a subordinate ranking (Armstrong et al. 2011). Similarly, access to shelter can lower baseline metabolic costs (Millidine et al. 2006), and this may increase the amount of energy available for growth. In contrast, although territorial individuals were not subordinate to active foragers in terms of aggressive interactions (they won and lost the same number of interactions with active foragers), they did show lower growth rates (7.9 mg d^{-1} ± 5.2 SE compared with 34±3.9 SE for territorial fish vs. active foragers, respectively). Collectively, these findings demonstrate that individuals with very different behavior, such as territoriality versus shelter-association, can have approximately equivalent growth performance. Conversely, individuals that appear to have equivalent dominance status can show very different growth performance depending on their level of mobility. Nevertheless, we note that growth rate is but one component of fitness. Under natural conditions, the lower foraging activity of territorial and shelter-associated fish might decrease mortality risk (e.g. due to predation), and hence enhance fitness, compensating for the lower growth performance of individuals that display these behaviors. We also note that habitats with higher flow velocity than that used in our experimental system might inflate the energy costs of active foraging and reduce the growth benefits of this behavioral strategy.

The growth benefits of territorial behavior depended on the predictability of food supply and also on the interaction of individual size with metabolic rate. Previous studies have shown that resource predictability can lead to increased levels of aggression and territoriality because such behavior allows dominant individuals to successfully defend resources (Grand and Grant 1994; Ryer and Olla 1995; McCarthy et al. 1999). However, such trends are not consistent among species, with other studies finding no relationship between the frequency of aggressive interactions and either food quantity or localization (Ryer and Olla 1996). One explanation for these inconsistencies is that competitor abundance can influence dominance behavior (e.g. Kaspersson et al. 2010) because the time and energy spent on aggression becomes uneconomical at high population densities (Grant 1993). In our study, social densities were quite high and territories are likely to have been a different shape than occurs in natural streams due to the shape of our experimental tanks. These factors potentially allowed territorial individuals to occasionally dart in and collect food while active foragers were otherwise occupied. Previous research on juvenile Atlantic salmon has shown that topographic complexity (Höjesjö et al. 2004) in combination with resource unpredictability (Reid et al. 2012) prevents dominant individuals from tracking, and monopolizing, resources. Our study suggests that, even in relatively simple aquaria, unpredictable food delivery enables sedentary individuals to obtain food while active foragers are occupying other areas.

Contrary to our expectations, we found no evidence that individuals with low RMRs were at an advantage when resources were limited. In fact, irrespective of food regime, fish with high metabolic rates had a distinct growth advantage because they were more likely to be active foragers and, if they instead displayed territorial behavior, they obtained a growth advantage that was not apparent for low RMR individuals. For active foragers, the increased potential for food-capture

associated with this behavior appears to have been sufficient to offset their higher metabolic rates and the higher energy costs related to increased swimming activity. An explanation for our finding that territoriality enhanced growth only for fish with high RMR is less obvious, particularly because juvenile trout with high and low RMR were equally likely to display territorial behavior. The literature demonstrates 2 disparate relationships between growth and RMR. Some studies have found a positive relationship that is mediated by behavior: individuals with high RMR can grow faster because they tend to be dominant and monopolize resources (Yamamoto et al. 1998). Conversely, others have found that individuals with low RMR can grow faster because their reduced maintenance costs increases scope for growth (e.g. Kooijman 2000). For instance, lizards from a high-elevation population with low RMR grew faster than their conspecifics from low elevation populations that had higher RMR (Sears 2005). The physiological mechanisms that cause individual variation in metabolic rate are generally poorly understood (see Burton et al. 2011a, 2011b). Our finding that high RMR individuals had higher growth than their low RMR siblings when expressing essentially the same behavior suggests that high RMR individuals have a larger metabolic machinery that allows faster food processing and assimilation (Biro and Stamps 2010) and/or higher growth efficiency. However, we cannot rule out the possibility that a down-regulation of RMR during the experimental period allowed territorial individuals (and active foragers) to maintain high growth when food was restricted. Metabolic rate and aggression have been shown to be temporally consistent for salmonid fishes (Cutts et al. 2001), but can also vary in response to environmental features such as availability of shelter (Millidine et al. 2006) or contact with conspecifics (Millidine et al. 2009). The high RMR fish in this study may, therefore, have down-regulated their metabolism when food was limited, thus maintaining growth by lowering RMR.

The range of among-individual variation in behavior observed among the brown trout in this study is similar to that observed in other salmonid fishes (Maclean et al. 2005; Reid et al. 2012). Nevertheless, dominance hierarchies with similar overall levels of aggression, activity, site fidelity, and shelter use formed irrespective of feeding regime, suggesting that individual behavior did not differ according to environment conditions. Previous studies indicate that the capacity for behavioral variation differs between species. For instance, foraging behavior and aggression of birds varies between locations with different food quality (MacNally and Timewell 2005), and aggression levels can be higher in contests over poor quality territories compared with territories with surplus food availability (Ewald 1985). Equivalent studies on fishes, however, have revealed conflicting results. In one study, juvenile chum salmon showed higher levels of aggression when food was delivered at a single point compared with scattered across a wide area (Ryer and Olla 1995). Similarly, charr (*Salvelinus malma* and *Salvelinus leucomaenis*) adopt a benthic or a drift foraging strategy depending on the abundance of drifting prey, with subordinate fish demonstrating a greater capacity for behavioral plasticity compared with dominants (Fausch et al. 1997). Conversely, and congruent with this study, investigations of coho and Atlantic salmon found no evidence of altered behavior in response to different food regimes (Ryer and Olla 1996; Maclean et al. 2005). Although we did not directly measure individual plasticity in behavior, our finding of a consistent central tendency and range of variation in behavior among feeding treatments suggests that juvenile trout do not strongly modify their behavior in response to food availability.

This study highlights the importance of behavior in determining the relative performance of individuals. Although ours was a laboratory-based study, the direction and magnitude of behavioral variation observed here is equivalent to that observed for related species under field and laboratory conditions (Adams et al. 1998; McLaughlin et al. 1999; Wilson and McLaughlin 2007). What we have uniquely shown is that different behavioral traits can result in approximately the same enhancement of individual growth, but that the manifestation of these benefits can depend on the predictability of food resources. Our tightly controlled experimental system allowed us to detect how subtle differences in individual behavior and physiology combine with environmental variation to influence growth performance. During the critical post-hatching phase, juvenile salmonid fishes experience high population densities and are subject to high mortality rates (Elliott 1990). Variation in behavior and physiology has been proposed as a "bet-hedging" mechanism to increase the range of microhabitats that individuals are able to exploit (Wilson 1998; Armstrong et al. 2011). Our results are partially consistent with the hypothesis that environmental variability promotes the coexistence of alternative behavioral phenotypes: the benefits of territoriality were only apparent when food resources were predictable. However, shelter use and active foraging behaviors enhanced growth irrespective of feeding regime, and we did not identify a set of conditions where fish with low RMR outperformed their high RMR siblings. Additional levels of environmental variation (e.g. topographic complexity of the habitat, Reid et al. 2012), or variation in predation risk associated with differences in foraging activity (e.g. Orpwood et al. 2006), may be required for juvenile trout with low RMR to attain higher fitness than their high RMR conspecifics.

FUNDING

National Environmental Research Council (UK) grant to N.B.M., J.D.A., and T.G.G.G.

We thank M. Miles, S. Keay, and J. Muir at Almondbank Hatchery and G. Law and T. Burton at the University of Glasgow for assistance with animal husbandry and experimental procedures. All experimental work was conducted in accordance with the ethical standards set by the Animals (Scientific Procedures) Act 1986, under UK Home Office Project License PPL 60/3625.

REFERENCES

Adams CE, Huntingford FA, Turnbull JF, Deattie C. 1998. Alternative competitive strategies and the cost of food acquisition in juvenile Atlantic salmon (*Salmo salar*). Aquaculture. 167:17–26.

Álvarez D, Nicieza AG. 2005. Is metabolic rate a reliable predictor of growth and survival of brown trout (*Salmo trutta*) in the wild? Can J Fish Aquat Sci. 62:643–649.

Ang TZ, Manica A. 2010. Benefits and costs of dominance in the angelfish *Centropyge bicolor*. Ethology. 116:855–865.

Armstrong, JD. & Nislow KH. 2006. Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo Salar*) and brown trout (*Salmo trutta*). Journal of Zoology, 269:403–413

Armstrong JD, Millidine KJ, Metcalfe NB. 2011. Ecological consequences of variation in standard metabolism and dominance among salmon parr. Ecol Freshw Fish. 20:371–376.

Bang A, Grønkjær P, Folkvord A. 2007. Possible fitness costs of high and low standard metabolic rates in larval herring, *Clupea harengus*, as determined by otolith microstructure. Mar Ecol Prog Ser. 331:233–242.

Bell AM. 2007. Future directions in behavioural syndromes research. Proc Biol Sci. 274:755–761.

Biro PA, Stamps JA. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol (Amst). 25:653–659.

Both C, Dingemanse NJ, Drent PJ, Tinbergen JM. 2005. Pairs of extreme avian personalities have highest reproductive success. J Anim Ecol. 74:667–674.
Brown JH, Ross B, McCauley S, Dance S, Taylor AC, Huntingford FA. 2003. Resting metabolic rate and social status in juvenile giant freshwater prawns, *Macrobrachium rosenbergii*. Mar Freshw Behav Physiol. 36:31–40.
Bryant DM, Newton AV. 1994. Metabolic costs of dominance in dippers, *Cinclus cinclus*. Anim Behav. 48:447–455.
Buchner AS, Sloman KA, Balshine S. 2004. The physiological effects of social status in the cooperatively breeding cichlid *Neolamprologus pulcher*. J Fish Biol. 65:1080–1095.
Burton T, Killen SS, Armstrong JD, Metcalfe NB. 2011a. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proc Biol Sci. 278:3465–3473.
Burton T, Hoogenboom MO, Armstrong JD, Groothuis TGG, Metcalfe NB. 2011b. Egg hormones in a highly fecund vertebrate: do they influence offspring social structure in competitive conditions? Funct Ecol. 25:1379–1388.
Careau V, Thomas D, Humphries MM, Réale D. 2008. Energy metabolism and animal personality. Oikos. 117:641–653.
Clarke RD. 1992. Effects of microhabitat and metabolic rate on food intake, growth and fecundity of two competing coral reef fishes. Coral Reefs. 11:199–205.
Cutts CJ, Adams CE, Campbell A. 2001. Stability of physiological and behavioural determinants of performance in Arctic char (*Salvelinus alpinus*). Can J Fish Aquat Sci. 58:961–968.
Dingemanse NJ, Réale D. 2005. Natural selection and animal personality. Behaviour. 142:1159–1184.
Elliott JM. 1975a. Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, *Salmo trutta* L. Freshw Biol. 5:287–303.
Elliott JM. 1975b. The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. J Anim Ecol. 44:823–842.
Elliott JM. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. II. Fish growth and size variation. J Anim Ecol. 59:171–185.
Ewald PW. 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. Anim Behav. 33:705–719.
Fausch KD, Nakano S, Kitano S. 1997. Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. Behav Ecol. 8:414–420.
Finstad AG, Forseth T, Ugedal O, Næsje TF. 2007. Metabolic rate, behavior and winter performance in juvenile Atlantic salmon. Funct Ecol. 21:905–912.
Grand TC, Grant JW. 1994. Spatial predictability of food influences its monopolisation and defence by juvenile convict cyclids. Anim Behav. 47:91–100.
Grant JW. 1993. Whether or not to defend? The influence of resource distribution. Mar Freshw Behav Phys. 23:137–153.
Grant JW, Kramer DL. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can J Fish Aquat Sci. 47:1724–1737.
Höjesjö J, Johnsson J, Bohlin T. 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (Salmo trutta) relative to subordinates. Behav Ecol Sociobiol. 56:286–289.
Kaspersson R, Höjesjö J, Pedersen S. 2010. Effects of density on foraging success and aggression in age-structured groups of brown trout. Anim Behav. 79:709–715.
Kooijman SALM. 2000. Dynamic energy and mass budgets in biological systems. Cambridge; Cambridge University Press.
Maclean A, Huntingford FA, Ruxton GD, Morgan IJ, Hamilton J, Armstrong JD. 2005. Testing the assumptions of the ideal despotic distribution with an unpredictable food supply: experiments in juvenile salmon. J Anim Ecol. 74:214–215.
MacNally R, Timewell CAR. 2005. Resource availability controls bird-assemblage composition through interspecific aggression. Auk. 122:1097–1111.
Martins TL, Roberts ML, Giblin I, Huxham R, Evans MR. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. Horm Behav. 52:445–453.
Martin-Smith KM, Armstrong JD. 2002. Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not dominance. J Anim Ecol. 71:413–423.
McCarthy ID, Gair DJ, Houlihan DF. 1999. Feeding rank and dominance in *Tilapia rendalli* under defensible and indefensible patterns of food distribution. J Fish Biol. 55:854–867.
McLaughlin RL, Grant JWA, Kramer DL. 1992. Individual variation and alternative patterns of foraging movements in recently-emerged brook charr (*Salvelinus frontinalis*). Behaviour. 120:286–301.
McLaughlin RL, Ferguson MM, Noakes DLG. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. Behav Ecol Sociobiol. 45:386–395.
Metcalfe NB, Taylor AC, Thorpe JE. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Anim Behav. 49:431–436.
Metcalfe NB, Valdimarsson SK, Morgan IJ. 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. J Appl Ecol. 40:535–544.
Metcalfe NB. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. J Fish Biol. 28:525–531.
Millidine KJ, Armstrong JD, Metcalfe NB. 2006. Presence of shelter reduces maintenance metabolism of juvenile salmon. Funct Ecol. 20:839–845.
Millidine KJ, Metcalfe NB, Armstrong JD. 2009. Presence of a conspecific causes divergent changes in resting metabolism, depending on its relative size. Proc Biol Sci. 276:3989–3993.
Nakano S. 1995. Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. J Anim Ecol. 64:75–84.
Nelson RJ. 2000. An introduction to behavioural endocrinology. Sunderland (MA); Sinauer.
Norman GR, Steinder DL. 2008. Biostatistics: the bare essentials. 3rd ed. Shelton (CT); PMPH USA.
Orpwood JE, Griffiths SW, Armstrong JD. 2006. Effects of food availability on temporal activity patterns and growth of Atlantic salmon. J Anim Ecol. 75:677–685.
R Development Core Team. 2010. R: a language and environment for statistical computing. Vienna (Austria); R Foundation for Statistical Computing.
Reid D, Armstrong JD, Metcalfe NB. 2012. The performance advantage of a high resting metabolic rate in juvenile salmon is habitat dependent. J Anim Ecol. 81:868–875. doi: 10.1111/j.1365-2656.2012.01969.x
Ryer CH, Olla BL. 1995. The influence of food distribution of the development of aggressiveness and competitive behaviour in juvenile chum salmon, *Oncorhynchus keta*. J Fish Biol. 46:264–272.
Ryer CH, Olla BL. 1996. Growth depensation and aggression in laboratory reared coho salmon: the effect of food distribution and ration size. J Fish Biol. 48:686–694.
Sears MW. 2005. Resting metabolic expenditure as a potential source of variation in growth rates of the sagebrush lizard. Comp Biochem Physiol, Part A Mol Integr Physiol. 140:171–177.
Senar JC, Polo VV, Uribe F, Camerino M. 2000. Status signalling, metabolic rate and body mass in the siskin: the cost of being a subordinate. Anim Behav. 59:103–110.
Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol (Amst). 19:372–378.
Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. Behav Ecol. 19:448–455.
Steingrimsson SO, Grant JWA. 2011. Determinants of multiple central-place territory use in wild young-of-the-year Atlantic salmon (*Salmo salar*). Behav Ecol Sociobiol. 65:275–286.
van Overveld T, Matthysen E. 2010. Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). Biol Lett. 6:187–190.
von Hulst D, Hutzelmeyer H, Kaetzke P, Khaschei M, Rödel HG, Schrutka H. 2002. Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). Behav Ecol Sociobiol. 51:245–254.
Wilson DS. 1998. Adaptive individual differences within single populations. Phil Trans R Soc Lond B. 353:199–205.
Wilson AD, McLaughlin RL. 2007. Behavioral syndromes in brook charr, *Salvelinus frontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. Anim Behav. 74:689–698.
Yamamoto T, Ueda H, Higashi S. 1998. Correlation among dominance status, metabolic rate and otolith size in masu salmon. J Fish Biol. 52:281–290.